

Effect of the host plant on the survivorship of parasitized *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) larvae and performance of its larval parasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae)

Mamoudou Sétamou^{a,b}, Nanqing Jiang^a, Fritz Schulthess^{a,*}

^a Stemborer Biological Control Program, ICIPE, P.O. BOX 30772-00100, G.P.O., Nairobi, Kenya

^b Beneficial Insect Research Unit, ARS-USDA, 2413 E Hgwy 83, Weslaco, TX 78596, United States

Received 3 June 2004; accepted 19 September 2004

Abstract

The effect of wild and cultivated gramineous hosts on the survivorship and weight of parasitized *Chilo partellus* larvae and on the performance of its larval parasitoid *Cotesia flavipes* were studied under laboratory conditions, in two experiments. In Experiment A, weight of *Ch. partellus* larvae offered to *Co. flavipes* was allowed to vary with host plant species in order to assess both the effect of weight and quality of larvae, as affected by the host plant, on the performance of the parasitoid. In Experiment B, larvae of similar weight across host plant species were selected to enable to separate the effect of weight from that of quality of the larvae. In Experiment A, the mean weight of larvae that produced cocoons varied significantly with plant species. In both experiments, the percentage of larvae producing cocoons and mean progeny size were lower and larvae died faster on wild than cultivated host plants. Immature development time of *Co. flavipes* tended to be higher on wild than cultivated grasses. The proportion of female progeny was highest on maize and lowest on the two sorghum species, in Experiment A, whereas in Experiment B, the sex ratio was similar between the host plant species. Similarly, egg-load of *Co. flavipes* offspring was highest on maize and lowest on Napier grass in Experiment A, but it did not vary significantly between host plants in Experiment B. It is suggested that in the coastal region of Kenya, perennial wild sorghum species are vital for the survival of *Co. flavipes* during the dry season, when superior plant hosts such as cultivated sorghum and maize are scarce.

© 2004 Elsevier Inc. All rights reserved.

Keywords: *Cotesia flavipes*; *Chilo partellus*; Parasitism; Host plant; Maize; Wild and cultivated sorghum; Napier grass; Tritrophic interaction

1. Introduction

In East and Southern African lowlands, the exotic stemborer *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) is the dominant and most damaging pest of maize and sorghum. *Cotesia flavipes* Cameron (Hymenoptera: Braconidae), a koinobiont endoparasitoid of

Ch. partellus larvae in Asia, was introduced into Kenya for a classical biological control program in 1993/94. It has become permanently established in the country, reducing borer densities by 50% and increasing maize yields by 10%, on an average (Overholt et al., 1997; Zhou et al., 2001). Following the success in Kenya, *Co. flavipes* was released in ten more countries in East and Southern Africa.

In Africa, maize is usually grown on small plots surrounded by land occupied by wild gramineous plants, which are natural hosts of stemborers (Bowden, 1976).

* Corresponding author. Fax: +254 20860110.

E-mail address: fschulthess@icipe.org (F. Schulthess).

Recent studies showed that most grass species are highly attractive to ovipositing female moths, although survival of immature stages is close to zero versus ca. 30% on maize (Khan et al., 1997a,b; Ofomata et al., 2000; Schulthess et al., 1997; Shanower et al., 1993). It was concluded that wild host species could act as trap plants rather than being a reservoir for pests as suggested earlier by Bowden (1976). This phenomenon was exploited by Khan et al. (1997a,b) in the ‘Push–Pull’ strategy, which involves trapping the pest on attractive host plant species for adult moths but unsuitable for larval development, and driving them away from the crop using repellent intercrops.

Schulthess et al. (2001) observed high parasitism of *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) eggs by *Telenomus* spp. (Hymenoptera: Scelionidae) during the dry season on wild hosts in the inland valleys in Benin, West Africa. Similarly, Ndemah et al. (2001), working in the forest zone of Cameroon, found a higher parasitoid species diversity on elephant grass *Pennisetum purpureum* Moench (Poaceae) than on maize. It was suggested that such wild hosts play an important role in maintaining stable parasitoid populations during the off-season and thereby lowering pest incidence in crop fields during the growing season (Ndemah et al., 2003). This was corroborated by Ndemah et al. (2002) with trials in Benin, which showed that in maize fields surrounded by border-rows of grasses, egg parasitism by *Telenomus* spp. and larval parasitism by the braconid *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) were increased significantly compared to sole maize fields.

Because *Co. flavipes* is a koinobiont species, parasitized host larvae continue to feed during the development of the parasitoid immatures within the host. Hailemichael (1998) and Jiang et al. (2004) showed that parasitized *Ch. partellus* larvae fed and continued to grow at the same rate as unparasitized ones on the same diet. Thus the species and thereby quality of the host plant might not only affect the stemborer host larvae, but also the parasitoids. Furthermore, the direct effect of the parasitoid on plant yield is probably negligible within one generation, and it was suggested that biological control takes place in the wild habitat (Schulthess et al., 1997).

The development of *Co. flavipes* in several stemborer species in Kenya has been studied by Ngi-Song et al. (1995), Ngi-Song and Overholt (1997), and Mbapila (1997), but no information exists on effects of the host plant species on the performance of parasitoids. The present study examines the potential host mediated effects of *Ch. partellus* feeding on four cultivated or wild host plants on the survival, development and performance of *Co. flavipes* in an attempt to elucidate the role of natural grass hosts in perennating the pest and its natural enemy.

2. Materials and methods

2.1. Insects

Chilo partellus larvae and *Co. flavipes* adults were obtained from a laboratory colony established at the International Center of Insect Physiology and Ecology (ICIPE); they originated from feral individuals collected from the coastal region of Kenya and southern Pakistan, respectively. Larvae of *Ch. partellus* were reared on an artificial diet described by Ochieng et al. (1985) at 25 °C, 50–80% relative humidity and a 12L:12D photoperiod. Colonies of *Co. flavipes* were maintained on *Ch. partellus* larvae as described by Overholt et al. (1994).

2.2. Host plants

Two cultivated annual crops (i.e., maize, *Zea mays* L., and sorghum, *Sorghum bicolor* L.) and two wild perennial grass species [i.e., wild sorghum, *Sorghum arundinaceum* (Desv.) Stapf, and Napier grass, *Pennisetum purpureum* (Schumacher) Pilg.], were used to rear *Ch. partellus*. Both wild grass species are used as fodder grasses in East and southern Africa (Skerman and RIVERS, 1990) and in addition, wild sorghum species is found to be the most important wild host plants of *Ch. partellus* followed by *Pennisetum* spp. (Le Rü, IRI-ICIPE, pers. comm.). Fresh stem pieces, 5-cm long, were collected from 2 month-old maize and sorghum plants grown under standard agronomic practices at the experimental fields of ICIPE, while pieces from wild host plants were collected from natural vegetation around ICIPE. These stem pieces were soaked for 5 min in a 0.035% solution of sodium hypochlorite for disinfection, then rinsed twice with distilled water and air-dried on sterile tissue paper in the laboratory before being infested with *Ch. partellus* larvae (Sétamou et al., 1993). The lower part of the stem was split to facilitate the insertion of *Ch. partellus*.

2.3. Experimental procedure

Two separate experiments were conducted. In the first (Experiment A), second instar *Ch. partellus* larvae were reared on each host diet for 7 days and weighed using a Mettler AE166 balance (Mettler, Toledo, Switzerland) before exposing them to 24-h-old, mated *Co. flavipes* females. To adjust for differences in mortality between diets, which was determined in a pre-experiment, 100 larvae were tested on maize and sorghum, 220 for wild sorghum, and 400 for Napier grass. The hand-stinging method described by Smith et al. (1993) was used to ensure parasitisation of each larva. Only one oviposition was allowed per larva and adult parasitoid. *Ch. partellus* larvae were thereafter singly placed in a glass vial containing a piece of host plant stem and

plugged with cotton wool. The vials were kept in a incubator at 26 °C, under 40–65% relative humidity and a 12L:12D photoperiod. The stem pieces were changed every two to three days until cocoon production or death of larvae.

In Experiment B, after feeding on the different diets for 8 days, larvae of similar weight across plant species were selected in order to assess the effect of quality of the diet rather than host insect size, which was expected to vary with food source, on the performance of the parasitoid. The initial number of *Ch. partellus* larvae used for each host plant species was the same and larvae were treated in the same way as described in Experiment A.

In both experiments, *Ch. partellus* larval survivorship was followed every 2–3 days at the time the diet was replaced during the first ten days, and on a daily basis thereafter. In addition, percentage of larvae successfully parasitized (i.e., forming cocoons) and of non-parasitized larvae (forming *Ch. partellus* pupae), percent parasitoid adult emergence from cocoons, egg to adult development time, and the progeny sex ratio were recorded for each diet. In both experiments, ten newly emerged female parasitoids per diet were randomly selected for assessment of egg load. These females were frozen for 30 min, and then dissected for egg counts in a 7.5% NaCl solution under a microscope. The potential growth index (PGI) of *Co. flavipes* for each diet was computed as the product of the percentage of stung larvae producing adult progeny and the sex ratio (i.e., mean proportion of female progeny) per diet, divided by the immature developmental period of the parasitoid (Sétamou, 1999).

2.4. Data analysis

Because the experimental procedures were slightly different, data from the two experiments were analysed separately. In each experiment, homogeneity of the survival curves of stung *Ch. partellus* larvae reared on the four host plants was examined using the LIFTEST procedure of SAS (SAS, 2000). Percentage successfully parasitized *Ch. partellus* larvae was compared

between treatments using a log-likelihood test (*G*-test), and host plants were discriminated using the closed-testing procedure (Hommel, 1988). A one-way analysis of variance (ANOVA) was used to examine the effect of host diets on *Ch. partellus* larval weight, immature developmental times of the parasitoid, egg-load of virgin adult females, and number of *Co. flavipes* progeny per host larva. Where significant *F* values were obtained, treatment means were separated using the Student–Newman–Keuls test (Zar, 1999). Linear regression model was used to examine the relationship between progeny and sex ratio of *Co. flavipes* with host larval weight.

3. Results

3.1. *Ch. partellus* larval weights

In Experiment A, larval weights varied significantly between the host plant diets after 7 days of feeding ($F = 37.4$, $df = 3$, $P < 0.0001$), with greatest larval weight obtained from sorghum stem cuttings, the smallest from Napier grass, and intermediate weights for larvae reared on maize and wild sorghum (Table 1). Larvae reared on cultivated sorghum were 2-fold heavier than the ones maintained on Napier grass. A similar trend was observed for weights of larvae that were successfully parasitized by *Co. flavipes* ($F = 5.43$, $df = 4$, $P < 0.0001$) and for their counterparts that died during the experiment ($F = 18.5$, $df = 3$, $P < 0.0001$). Successfully parasitized larvae were significantly heavier than those that died in the two wild host plants, but not in the cultivated ones, i.e., maize and sorghum (Table 1). In Experiment B, where larvae were selected for similar size, weights of larvae did not vary significantly between host plant species (Table 1; $F = 2.14$, $df = 3$, $P = 0.10$).

3.2. Survivorship of *Ch. partellus* and development of *Co. flavipes* on different host plants

In Experiment A, the survivorships of *Ch. partellus* stung by *Co. flavipes* significantly varied with the host

Table 1

Weight (mg) \pm SE of *Ch. partellus* larvae at the time of parasitization (Experiments A and B), and weight of larvae that produced *Co. flavipes* cocoons, and that died of unknown reasons on different host plant species in Experiment A

Host diets	Experiment A				Experiment B	
	All larvae	<i>N</i>	Larva that formed cocoons	Larva that died for unknown reason	All larva	<i>N</i>
<i>Z. mays</i>	12.8 \pm 0.6b	86	12.7 \pm 0.6bA	12.8 \pm 0.9bA	29.5 \pm 1.5a	63
<i>S. bicolor</i>	17.5 \pm 1.6a	46	19.7 \pm 2.3aA	15.4 \pm 2.2aA	34.2 \pm 1.5a	67
<i>S. arundinaceum</i>	13.6 \pm 0.5b	107	16.8 \pm 1.6abA	13.0 \pm 0.4bB	31.3 \pm 2.2a	44
<i>P. trachyphyllum</i>	8.1 \pm 0.3c	133	12.7 \pm 1.2bA	7.8 \pm 0.3cB	27.0 \pm 2.8a	46

Means within columns followed by the same lower case letter and means within row followed by the same capital letter are not significantly different (SNK test, $P < 0.05$). *N* is the total number of larvae used for the stinging of the parasitoid.

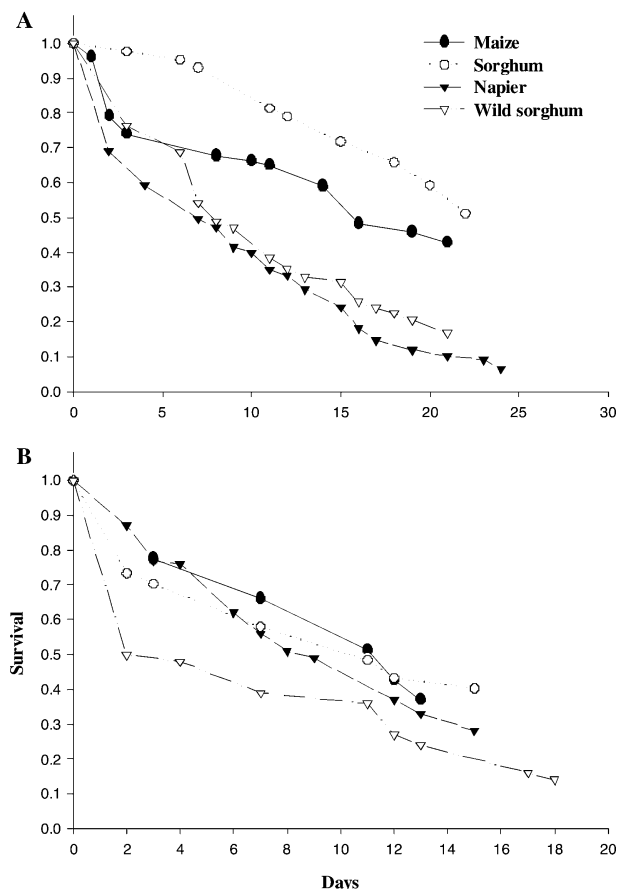


Fig. 1. Survivorship of parasitized *Ch. partellus* larvae in Experiment A, where larval weight varied and Experiment B where larval weight was kept constant across plant species.

plant species (Wilcoxon test; $\chi^2 = 45.1$, $df = 3$, $P < 0.0001$). Larval survivorship was lowest on the wild host plants, intermediate on maize and highest on sorghum (Fig. 1A). In Experiment B, larval survivorship on wild sorghum was significantly lower than those recorded on maize, sorghum and Napier grass (Wilcoxon test; $\chi^2 = 10.8$, $df = 3$, $P = 0.013$), but no significant difference could be detected between these three latter host plants (Fig. 1B).

In Experiment A, the percentage of larvae successfully parasitized by *Ch. partellus* was highest for larvae reared on cultivated grasses, intermediate on wild sorghum and lowest on Napier grass ($G = 281.7$, $df = 3$,

$P < 0.0001$; Table 2). The same trend was observed in Experiment B ($G = 943.8$, $df = 3$, $P < 0.0001$), but Napier grass had the intermediate percentage of larvae successfully parasitized, and the lowest was recorded on wild sorghum (Table 2). In both experiments, the emergence rate of adult parasitoids from cocoons was high and similar among host plants except on Napier grass in Experiment B, where it was significantly lower than in the three other hosts (Experiment A: $F = 0.95$, $df = 3$, $P = 0.42$; Experiment B: $F = 7.8$, $df = 3$, $P = 0.0002$) (Table 2). Percentage of larvae producing *Co. flavipes* cocoons significantly varied between experiments A and B ($G = 16.5$, $df = 1$, $P < 0.0001$) while adult emergence from cocoon was similar for the two experiments ($G = 3.5$, $df = 1$, $P > 0.5$).

In Experiment A, the development time of *Co. flavipes* immatures within *Ch. partellus* larvae was significantly affected by the host larval diet ($F = 8.4$, $df = 3$, $P < 0.0001$) and ranged from 15 days on the two sorghum species to 23 days on Napier grass (Table 3). Likewise, the total immature development period (from egg to adult) of *Co. flavipes* followed the same trend; total development time was comparable on maize and the two sorghum species, but longest on Napier grass ($F = 13.4$, $df = 3$, $P < 0.0001$) (Table 3). In Experiment B, egg-to-cocoon development time was shorter on cultivated than wild host plants ($F = 3.34$, $df = 3$, $P = 0.025$). A similar trend was observed in the total immature development time (Table 3).

3.3. Progeny, egg-load, and potential growth index of *Co. flavipes*

In both experiments, the brood size of *Co. flavipes* significantly varied with the host larval diet (Table 3). In Experiment A, the number of *Co. flavipes* adults emerged per larva was highest on maize, intermediate on sorghum and Napier grass, and lowest on wild sorghum. A covariance analysis showed that only host larval diet ($F = 7.44$, $df = 3$, 53, $P = 0.0003$) and not host larval weight ($F = 1.31$, $df = 1$, 53, $P = 0.25$) significantly affected the number of adults emerged. Similarly, the brood sex ratio significantly varied with the host plant species used as diet ($F = 4.02$, $df = 3$, 50, $P = 0.012$), with a significantly higher proportion of female progeny obtained from larvae maintained on maize compared to other host plants

Table 2

Percentage of *Ch. partellus* forming cocoons, unexplained larval mortality and *Co. flavipes* adult emergence on various host plant species in Experiments A and B

	Cocoon formation		Mortality		Adult emergence	
	A	B	A	B	A	B
<i>Z. mays</i>	42.7a	38.1a	57.3a	60.3a	97.1a	91.7a
<i>S. bicolor</i>	51.2a	40.3a	48.8a	53.7a	81.8a	96.3a
<i>S. arundinaceum</i>	16.7b	13.6b	83.3b	86.4b	93.7a	83.3a
<i>P. trachyphyllum</i>	6.5b	28.3ab	93.5b	71.7ab	87.5a	69.2b

Means within columns followed by the same lower case letter are not significantly different (SNK test, $P < 0.05$).

Table 3

Immature developmental time, number progeny per host larva and sex ratio (SR) as a proportion of females (means \pm SE) of *Co. flavipes* parasitizing *Ch. partellus* larvae feeding on different host plants in Experiments A and B

Host diets	Immature development time in days			Progeny	SR
	Egg-cocoon	Cocoon-adult	Total		
Experiment A					
<i>Z. mays</i>	16.9 ± 0.7b	6.3 ± 0.2a	22.9 ± 0.6b	24.6 ± 3.3a	0.78 ± 0.04a
<i>S. bicolor</i>	14.9 ± 0.6b	6.9 ± 0.2a	20.9 ± 0.4b	13.4 ± 2.4b	0.21 ± 0.07c
<i>S. arundinaceum</i>	15.1 ± 0.8b	7.0 ± 0.4a	21.8 ± 0.6b	7.9 ± 1.5b	0.26 ± 0.08c
<i>P. trachyphyllum</i>	22.5 ± 2.3a	7.1 ± 0.6a	29.6 ± 2.2a	16.3 ± 2.3b	0.52 ± 0.10b
Experiment B					
<i>Z. mays</i>	11.8 ± 0.3a	6.9 ± 0.1a	18.7 ± 0.3b	30.6 ± 3.55a	0.71 ± 0.07a
<i>S. bicolor</i>	12.1 ± 0.2a	6.2 ± 0.1b	18.4 ± 0.2b	33.7 ± 3.37a	0.71 ± 0.05a
<i>S. arundinaceum</i>	14.3 ± 1.8a	5.8 ± 0.2bc	20.6 ± 2.2a	10.6 ± 2.77b	0.71 ± 0.18a
<i>P. trachyphyllum</i>	14.1 ± 1.1a	5.3 ± 0.4c	17.4 ± 0.6b	10.7 ± 1.72b	0.54 ± 0.11a

Means within columns and experiment followed by the same lower case letter are not significantly different (SNK test, $P < 0.05$).

Table 4

Mean egg load \pm SE and potential growth index of *Co. flavipes* females from *Ch. partellus* larvae fed on different diets

Host diets	A		B	
	Egg load	PGI	Egg load	PGI
<i>Z. mays</i>	154.6 \pm 1.8a	0.356	139.2 \pm 6.3a	0.463
<i>S. bicolor</i>	124.1 \pm 4.5b	0.062	128.8 \pm 6.3a	0.519
<i>S. arundinaceum</i>	131.1 \pm 5.0b	0.016	133.0 \pm 6.1a	0.050
<i>P. trachyphyllum</i>	92.7 \pm 4.3c	0.015	131.6 \pm 5.7a	0.059

Means within columns followed by the same lower case letter are not significantly different (SNK test, $P < 0.05$). PGI = stung larvae producing adult progeny (%) \times female progeny (per host larva)/the total developmental period of the parasitoid.

(Table 3). However, the significant host plant species by *Ch. partellus* larval weight interaction ($F = 3.03$, $df = 3$, 50, $P = 0.03$) suggested that the effect of host weight on *Co. flavipes* progeny and sex ratio varied with the host plant. Larval weight positively and significantly affected the proportion of female progeny on Napier grass and sorghum ($y = 0.0175x - 0.15$, $R^2 = 0.37$, $P = 0.007$). Egg-load of female *Co. flavipes* offspring was highest on maize, lowest on Napier grass and similar on the two sorghum species (Table 4; $F = 75.33$, $df = 3$, $P < 0.0001$).

In Experiment B, no significant differences were detected between host plant species for *Co. flavipes* sex ratio ($F = 0.85$, $df = 3$, $P < 0.47$) (Table 3) and egg-load ($F = 52$, $df = 3$, $P = 0.47$) (Table 4).

In Experiment A, the potential growth index of *Co. flavipes* was highest on maize and considerably lower on sorghum and the two wild host plants, while in Experiment B, it was similar on the two cultivated hosts and much lower but similar on the wild host plants (Table 4).

4. Discussion

Because hosts continue to feed after parasitization, the amount and quality of host diet can affect the performance of koinobiont parasitoids. The differential survivorships of parasitized *Ch. partellus* suggest that host plant species significantly affect the rate of successfully

parasitized larvae by *Co. flavipes*. On wild host plant species, parasitized *Ch. partellus* larvae died faster than on maize or cultivated sorghum. Consequently, the percentage of larvae yielding *Co. flavipes* cocoons was lower on the two wild host plant species compared to maize and sorghum. The higher mortality of parasitized *Ch. partellus* larvae on wild host plants could partly be attributed to the initial smaller host sizes at stinging by *Co. flavipes*. Ngi-Song et al. (1995) reported that the proportion of successfully parasitized *Ch. partellus* larvae by *Co. flavipes* was higher in larger (i.e., 4th and 5th instars) than smaller larvae (i.e., 3rd instar). Similar results were obtained for *Chilo orichalcociliellus* Strand (Lepidoptera: Crambidae) parasitized by *Cotesia chilonis* (Matsumura) (Hymenoptera: Braconidae) (Okech and Overholt, 1996). *Co. chilonis* was even unable to complete development in smaller 1st and 2nd instar *Ch. orichalcociliellus*, as all parasitized larvae died before cocoon emergence (Kajita and Drake, 1969). However, in Experiment B host larvae were of similar size at stinging but significantly more larvae yielded *Co. flavipes* on maize and sorghum than the wild host plant species. These results suggest that other factors than the size of host larva at parasitization influence the successful completion of *Co. flavipes* development in *Ch. partellus* maintained on the various host plants.

In studies on the effects of host plant species on the performance of *Ch. partellus*, Mohamud (1997) and

Ofomata et al. (2000) observed that survivorship of unparasitized *Ch. partellus* larvae was highest on maize followed by sorghum and less than 10% on wild grasses. Similar results were obtained by Shanower et al. (1993) for the African cereal stemborer species *S. calamistis* and *Eldana saccharina* Walker (Lepidoptera: Pyralidae); larval mortality was close to 100% on wild hosts except for wild sorghum which yielded 5% pupation. However, in the latter two studies, the experiment was initiated with neonate larvae, which, before penetrating into the stem, fed on the epidermis of leaves or leaf sheaths, which is high in silica. Silica is known to have a negative effect on the bionomics of stemborers and especially young instars, and concentrations are much higher in rice and wild grasses than maize (i.e., up to 12 versus 2.5%, respectively) (Panda et al., 1975; Sasamoto, 1965; Sétamou et al., 1993). This might have accounted for the high larval mortality of close to 100% found by Shanower et al. (1993) on wild grasses. In the present study however, stem cuttings were infested with 2nd instars, which never fed on the epidermis of the stem or leaves. In contrast to silica, nitrogen leads to tilting of balance of the carbon/nitrogen (C/N) ratio in plants (Singh and Singh, 1969), resulting in thinner cell walls, softer and succulent tissue. Sétamou et al. (1993) showed that lower *S. calamistis* mortality was associated with N fertilisation. According to Bernays and Barbehenn (1987), wild grasses generally contained lower N compared to cultivated ones. However, fodder grasses were selected for their high nutrient content and digestibility, and their crude protein contents are at the level of those of cultivated sorghum and maize (Skerman and Riveros, 1990). Artificial selection in cultivated plants is also known to have reduced the level of secondary compounds rendering the plant more susceptible to herbivores (Evans, 1993), which could partly explain the higher survival of host larvae on maize and sorghum than wild host plants. Also, grasses contain low levels of secondary compounds, which, in addition, do not have toxic effects (Bernays and Chapman, 1977; Jung and Batzli, 1979; Mole and Joern, 1994; Owen and Wiegert, 1981).

In addition to the effect on host larva survival, host plant species affected the progeny production, the development time, and the sex ratio of the parasitoid. The brood size and the sex ratio were higher on maize and sorghum, whereas the development time tended to be longer on wild host plants. This suggests that the quality of host larvae is of paramount importance in the performance of *Co. flavipes*. Natural enemies of phytophagous insects function and develop in a multi-trophic context (Price et al., 1980). Thus their behavior and physiology, which determine their fitness, are influenced by many factors and stimuli derived from the plant (first trophic level) and the phytophagous host (second trophic level) (Takabayashi et al., 1991; Vinson, 1976). Several authors reported that the performance of a parasitoid is nega-

tively affected by allelochemicals in the host diet (Barbosa et al., 1986, 1990; Duffey et al., 1986; Godfray, 1994; Sznajder and Harvey, 2003). Parasitoids are generally more susceptible to toxic compounds than their phytophagous hosts, because they are incapable of metabolizing plant secondary compounds present in their host (Campbell and Duffey, 1979; Quicke, 1997). This effect is especially expressed in koinobiont endoparasitoids whose larva develops in a host, which continues to feed and grow after having been parasitized (Askew and Shaw, 1986). As proposed by Waage (1982) differences in host quality and size might also have affected size of the female adult parasitoid, as indicated by the differences in egg-load in Experiment A, thus the host plant might have a long-term effect on the fitness of the parasitoid population.

In Experiment B, sex ratio did not vary significantly with plant species, indicating that the proportion of fertilized eggs oviposited in a host by *Co. flavipes* was not determined by host quality. In Experiment A, however, host size was positively related to sex ratio on sorghum only, and wild sorghum, which had the lowest mean larval weight, yielded the second highest sex ratio. As pointed out by Strand (1985), fitness of one sex—female in this case—might be more adversely affected by host size and quality than the other, and mortality of the female parasitoid during development might have varied with host plant species.

In East Africa, *Co. flavipes* was released and became established first in the coastal area of Kenya in 1993 (Overholt et al., 1994; Overholt, 1998). Besides *Ch. partellus*, it attacks the two minor native stemborer species *S. calamistis* and *Ch. orichalcociliellus* Strand, but parasitisation rates are considerably lower than on its natural host *Ch. partellus* (Zhou et al., 2003). Surveys in coastal Kenya showed that *Ch. partellus* survived on wild sorghum and Napier grass (Mbapila, 1997). Similarly, in recent intensive surveys on wild grasses in Kenya, 95% of *Chilo* spp. and nearly 100% of all *Ch. partellus* larvae were found on wild sorghum species and a few on *Pennisetum* and *Panicum* spp. (B. LeRü, IRD-ICIPE, pers. comm.). It is suggested that *Co. flavipes* survived the dry season parasitizing *Ch. partellus* and the two indigenous stemborer species in the few maize fields planted near rivers and on wild annual sorghum species, which are very abundant in the coastal area of Kenya (P. Owuor, ICIPE, pers. comm.).

As fodder grasses are low in secondary compounds and high in crude protein, the question arises what could have caused the differences in suitability of the host plant species used in the present study to *Ch. partellus* larvae. A survey in southern Benin by Baba-Moussa (1998) showed that maize stems commonly harbored endophytic fungi such as *Acremonium* sp. and *Fusarium verticillioides* Sacc. (Nirenberg). Grass endophytes such as *Acremonium* spp. often have beneficial mutualistic effects

because they enhance growth via increased tillering and increased insect resistance (Bacon and Hill, 1996). By contrast, Schulthess et al. (2002) and Ako et al. (2003) showed that ovipositing female borers are attracted to maize plants infected with the fungus and that the progenies feeding on such plants had higher survival and higher fecundity. Future studies should investigate whether there are differences in the susceptibility to the different endophytic fungi between gramineous plant species and whether and how they affect the performance of both the pest and its parasitoids.

Acknowledgements

The authors wish to thank Gerphas Okuku and John Obala for their technical assistance during the experiments. The work was funded by the Directorate General for International Cooperation, The Netherlands.

References

- Ako, M., Schulthess, F., Gumedzoe, M.Y.D., Cardwell, K.F., 2003. The effect of *Fusarium verticillioides* Sacc. (Nirenberg) on oviposition behaviour and bionomics of lepidopteran and coleopteran pests attacking the stem and cobs of maize in West Africa. *Entomol. Exp. Appl.* 106, 201–210.
- Askew, R.R., Shaw, M.R., 1986. Parasitoid communities: their size, structure and development. In: Waage, J.K., Greathead, D. (Eds.), *Insect Parasitoids*. Academic Press, London, UK, pp. 225–264.
- Baba-Moussa, A.A.M.T., 1998. La Microflore Associée aux Dégâts des Lépidoptères Foreurs de tiges et Mineurs d'Epis de Maïs (*Zea mays*) dans la Région Sud du Bénin avec Référence Spéciale *Fusarium moniliforme* Sheld. Mémoire d'Ingénieur Agronome, Option Production Végétale. Université du Bénin, Lomé Togo. 93p.
- Bacon, C.W., Hill, N.S., 1996. Symptomless grass endophytes: products of coevolutionary symbioses and their role in the ecological adaptations of grasses. In: Redlin, S.C., Carris, L.M. (Eds.), *Endophytic Fungi in Grasses and Woody Plants: Systematics, Ecology, and Evolution*. APS Press, The American Phytopathological Society St. Paul, Minnesota, pp. 155–178.
- Barbosa, P., Kemper, J., Gross, P., Martinat, P., 1990. Influence of dietary nicotine and colony source of *Manduca sexta* (Lepidoptera: Sphingidae) on its suitability as a host of *Cotesia congregata* (Hymenoptera: Braconidae). *Entomophaga* 35, 223–231.
- Barbosa, P., Saunders, J.A., Kemper, J., Trumbule, R., Olechno, J., Martinat, P., 1986. Plant allelochemicals and insect parasitoids: effects of nicotine on *Cotesia congregata* and *Hyposoter annulipes*. *J. Chem. Ecol.* 12, 1319–1328.
- Bernays, E.A., Chapman, R.F., 1977. Deterrent chemicals as a basis of oligophagy in *Locusta migratoria* (L). *Ecol. Entomol.* 2, 1–18.
- Bernays, E.A., Barbehenn, R., 1987. Nutritional ecology of grass foliage chewing insect pests. In: Slansky, Jr., F.Rodriguez, (Eds.), *Nutritional ecology of insects, mites, spiders and related invertebrates*. Wiley, New York, pp. 147–175.
- Bowden, J., 1976. Stem borers ecology and strategy for control. *Ann. Appl. Biol.* 84, 107–111.
- Campbell, B.C., Duffey, S.S., 1979. Tomatine and parasitic wasps. Potential incompatibility of plant antibiosis with biological control. *Science* 205, 700–702.
- Evans, L.T., 1993. *Crop evolution, adaptation and yield*. Cambridge University Press, Cambridge UK.
- Duffey, S.S., Bloem, K.A., Campbell, B.C., 1986. Consequences of sequestration of plant natural products in plant–insect–parasitoid interactions. In: Boethel, D.J., Eikenbary, R.D. (Eds.), *Interactions of Plant Resistance and Parasitoids and Predators of Insects*. Horwood Press, Chichester, UK, pp. 31–60.
- Godfray, H.C.J., 1994. In: Krebs, J.R., Clutton-Brock, T. (Eds.), *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, Princeton, NJ 473pp.
- Hailemichael, Y., 1998. Comparative evaluation of *Cotesia chilonis*, *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae) as potential biological control agents against gramineous stemborers in West Africa. Ph.D. dissertation, Texas A&M University.
- Hommel, G., 1988. A stagewise rejective multiple test procedure based on a modified Bonferroni test. *Biometrika* 75, 383–386.
- Jiang, N., Sétamou, M., Ngi-Song, A.J., Omwega, C.O., 2004. Performance of *Cotesia flavipes* (Hymenoptera: Braconidae) in parasitizing *Chilo partellus* (Lepidoptera: Crambidae) as affected by temperature and host stage. *Biol. Control* 31, 155–164.
- Jung, H.J., Batzli, G.O., 1979. Patterns in the Phytochemistry of arctic plants. *Biochem. System. Ecol.* 7, 203–209.
- Kajita, H., Drake, E.F., 1969. Biology of *Apanteles chilonis* and *A. flavipes* (Hymenoptera: Braconidae), parasites of *Chilo suppressalis*. *Mushi* 42, 163–179.
- Khan, Z.R., Ampong-Nyarko, K., Chiliswa, P., Hassanali, A., Kimani, S., Lwande, W., Overholt, W.A., Pickett, J.A., Smart, L.E., Wadhams, L.J., Woodcock, M., 1997a. Intercropping increases parasitism of pests. *Nature* 388, 631–632.
- Khan, Z.R., Chiliswa, P., Ampong-Nyarko, K., Smart, L.E., Polaszek, A., Wandera, J., Mulaa, M.A., 1997b. Utilisation of wild gramineous plants for management of cereal stemborers in Africa. *Insect Sci. Appl.* 17, 143–150.
- Mbapila, J.C., 1997. Comparative seasonal adaptation of *Cotesia flavipes* Cameron and *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae) to *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae) on the Kenya coast. Ph.D. dissertation, University of Dar-Es-Salaam, Tanzania.
- Mohamud, M.H., 1997. Survival and development of the stemborer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) on selected wild gramineous plants. M.Sc. thesis, Kenyatta University, Nairobi, Kenya. 77pp.
- Mole, S., Joern, A., 1994. Feeding behaviour of graminivorous grasshoppers in response to host-plant extracts, alkaloids and tannins. *J. Chem. Ecol.* 20, 3097–3109.
- Ndemah, R., Schulthess, F., Poehling, M., Borgemeister, C., 2001. Natural enemies of lepidopterous borers on maize and elephant grass in the forest zone of Cameroon with special reference to *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *Bull. Ent. Res.* 91, 205–212.
- Ndemah, R., Gounou, S., Schulthess, F., 2002. The role of wild grasses in the management of lepidopterous stem-borers on maize in the humid tropics of western Africa. *Bull. Ent. Res.* 92, 507–519.
- Ndemah, R., Schulthess, F., Korie, S., Borgemeister, C., Poehling, M., Cardwell, K.F., 2003. Factors affecting infestations of the stalk borer *Busseola fusca* (Fuller) on maize in the forest Zone of Cameroon with special reference to scielonid egg parasitoids. *Environ. Entomol.* 32, 61–70.
- Ngi-Song, A.J., Overholt, W.A., 1997. Host selection by *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae): an example of tritrophic relationship in a grass-stem borer parasitoid system. *Proceedings of a CTA/IAR/IIBC seminar*, CTA, 172–181.
- Ngi-Song, A.J., Overholt, W.A., Ayertey, J.N., 1995. Suitability of African gramineous stemborers for the development of *Cotesia flavipes* and *Cotesia sesamiae* (Hymenoptera: Braconidae). *Environ. Entomol.* 24, 978–984.

- Ochieng, R.S., Onyango, F.O., Bungu, M.D.O., 1985. Improvement of techniques for mass culture of *Chilo partellus* (Swinhoe). Insect Sci. Appl. 6, 425–428.
- Ofomata, V.C., Overholt, W.A., Lux, S.A., Huis, A., Egwuatu, R.I., 2000. Comparative studies on the fecundity, egg survival, larval feeding, and development of *Chilo partellus* and *Chilo orichalcociliellus* (Lepidoptera: Crambidae) on five grasses. Ann. Entomol. Soc. Am. 93, 492–499.
- Okech, S.H.O., Overholt, W.A., 1996. Comparative biology of *Cotesia chilonis* (Hymenoptera: Braconidae) on selected African gramineous stem borers. Biocontrol Sci. Technol. 6, 595–602.
- Overholt, W.A., Ochieng, J.O., Lammers, P.M., Ogedah, K., 1994. Rearing and field release methods for *Cotesia flavipes* Cameron (Hymenoptera: Braconidae), a parasitoid of tropical gramineous stem borers. Insect Sci. Appl. 15, 253–259.
- Overholt, W.A., Ngi-Song, A.J., Omwega, C.O., Kimani-Njogu, S.W., Mbapila, J., Sallam, M.N., Ofomata, V.C., 1997. A review of the introduction and establishment of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) in East Africa for biological control of cereal stem borers. Insect Sci. Appl. 17, 79–95.
- Overholt, W.A., 1998. Biological control. In: Polaszek, A. (Ed.), Cereal stem borers in Africa: Taxonomy, Natural Enemies, and Control. CAB International, Wallingford, UK, pp. 349–362.
- Owen, D.F., Wiegert, R.G., 1981. Mutualism between grass and grazers: An evolutionary hypothesis. Oikos 36, 376–378.
- Panda, N., Pradhan, B., Samalo, A.P., Rao, P.S.P., 1975. Note on the relationship of some biochemical factors with the resistance in rice varieties to yellow rice borer. Indian J. Agric. Sci. 45, 499–501.
- Price, P.W., Bouton, C.E., Gross, P., McPherson, B.A., Thompson, J.N., Weis, A.E., 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Annu. Rev. Ecol. Syst. 11, 41–65.
- Quicke, D.L.J., 1997. Parasitic wasps. Chapman & Hall, London.
- SAS Institute, 2000. Users' guide: Statistics, release 8.0 ed. SAS Institute, Cary, NC.
- Sasamoto, K., 1965. Resistance of the rice plant applied with silicate and nitrogenous fertilizers to the rice stem borer, *Chilo suppressalis* Walker. Proceedings of the Faculty of Liberal Arts Education3, Yamanashi University, Japan No.3, pp. 73.
- Schulthess, F., Bosque-Pérez, N.A., Chabi-Olaye, A., Gounou, S., Ndemah, R., Goergen, G., 1997. Exchange of natural enemies of lepidopteran cereal stem borers between African regions. Insect Sci. Appl. 17, 97–108.
- Schulthess, F., Chabi-Olaye, A., Goergen, G., 2001. Seasonal fluctuations of noctuid stem borer egg parasitism in southern Benin with special reference to *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Telenomus* spp. (Hymenoptera: Scelionidae) on maize. Biocontrol Sci. Technol. 11, 765–777.
- Schulthess, F., Cardwell, K.F., Gounou, S., 2002. The effect of endophytic *Fusarium verticillioides* on infestation of two maize varieties by lepidopterous stem borers and coleopteran grain feeders. Phytopathology 92, 120–128.
- Sétamou, M., 1999. Ecology and pest status of *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae), a cob borer of maize in West Africa. Ph.D. thesis, Hanover University.
- Sétamou, M., Schulthess, F., Bosque-Pérez, N.A., Thomas-Odjo, A., 1993. Effect of plant nitrogen and silica on the bionomics of *Sesamia calamistis* (Lepidoptera: Noctuidae). Bull. Entomol. Res. 83, 405–411.
- Shanower, T.G., Schulthess, F., Bosque-Pérez, N.A., 1993. The effect of larval diet on the growth and development of *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Eldana saccharina* Walker (Lepidoptera: Pyralidae). Insect Sci. Appl. 14, 681–685.
- Singh, T.P., Singh, R., 1969. Incidence of stem borer (*Chilo zonellus* Swinhoe) and lodging in Jaunpur variety of maize under different fertility levels of nitrogen. Indian J. Entomol. 31, 158–160.
- Skerman, P.J., Riveros, F., 1990. Tropical grasses. Food and Agricultural Organization of the United Nations, Rome pp. 323.
- Smith Jr., J.W., Wiedenmann, R.N., Overholt, W.A., 1993. Parasites of lepidopteran stem borers of tropical gramineous plants. ICIPE Science Press, Nairobi, Kenya pp. 89.
- Strand, M.R., 1985. The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. In: Waage, J., Greathead, D. (Eds.), Insect Parasitoids, 13th Symposium of the Royal Entomological Society of London, 18–19 September, 1985, London.
- Sznajder, B., Harvey, J.A., 2003. Second and third trophic level effects of differences in plant species reflect dietary specialisation of herbivores and their endoparasitoids. Entomol. Expl. Appl. 109, 73–82.
- Takabayashi, J., Dicke, M., Posthumus, M.A., 1991. Variation in composition of predator-attracting allelochemicals emitted by herbivore-infested plants/relative influence of plant and herbivore. Chemoecology 2, 1–6.
- Vinson, S.B., 1976. Host selection by insect parasitoids. Annu. Rev. Entomol. 37, 141–172.
- Waage, J.K., 1982. Sex ratio and population dynamics of natural enemies: some possible interactions. Ann. Appl. Biol. 101, 159–164.
- Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall, Upper Saddle River, New Jersey.
- Zhou, G., Baumgartner, J., Overholt, W.A., 2001. Impact assessment of an exotic parasitoid on (Hymenoptera: Braconidae) stem borer (Lepidoptera) population dynamics in Kenya. Ecol. Appl. 11, 1554–1562.
- Zhou, G., Overholt, W.A., Kimani-Njogu, S.W., 2003. Species richness and parasitism in an assemblage of parasitoids attacking maize stem borers in coastal Kenya. Ecol. Entomol. 28, 109–118.